The Structure and Development of *Marchasta areolata* Camp.

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Summary

Details are given regarding the structure and development of the thallus and also of the antheridium, the archegonium and the sporogonium of *Marchasta areolata* Camp. The problem of the classification of *Marchasta* is discussed.

Introduction

Marchasta areolata Camp. was described by the writer in a previous paper (Campbell, 1954) as a new monotypic genus of the Marchantiaceae. In the present paper details are given regarding structure and development, and the affinities of the new genus are discussed.

The material on which the paper is based was collected in October, 1953 at Waiho, South Westland from the same clan as the type specimen. In order to obtain all stages in development some of the plants were kept growing for two months in the cool glasshouse at Massey Agricultural College.

The Structure and Development of the Thallus

The thallus has a midrib region on its ventral side (figs. 1, 2 and 3). This midrib is a compact, almost colourless zone, with its free surface plano-convex in outline. It is about twenty cells deep at the thickest part and gradually becomes thinner as it merges into the wings Its cells are elongated in a sagittal plane being four times as long as they are broad. There are no oil bodies or fungal hyphae present.

The dorsal portion of the thallus in the midrib region and the whole depth of the thallus in the wings consists of loose green tissue with large air chambers (figs. 1, 2 and 3) The air chambers are curved and extend from the midrib to the dorsal epidermal layer of cells. The marginal air chambers are the longest and extend from the sides of the midrib to the dorsal surface near the margin of the thallus, those nearer the mid-line are progressively shorter and extend from the midrib to regions of the dorsal surface progressively nearer the mid-line The air chambers of the wings radiate out towards the margin, but those above the midrib curve upwards in an anterior direction (fig. 2). Viewed from the ventral side the wings appear to be marked with dark green lines radiating outwards from the midrib and joining up with each other near the margin (fig. 4). These lines represent the partitions between the air chambers, and the paler bands between them represent the air chambers themselves Viewed from the dorsal side the thallus has a flecked appearance It is of a pale green colour marked into polygonal areas by lines of deeper green (fig 5) The green lines represent the partitions between the air chambers, lying more or less vertical as they curve upwards to the dorsal surface of the thallus The pale green areas represent the dorsal ends of the air chambers. Transverse and vertical sections of the

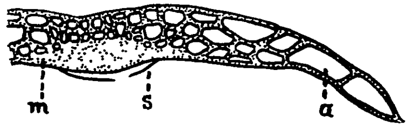
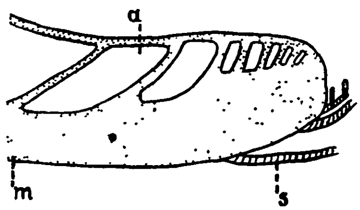


Fig. 1



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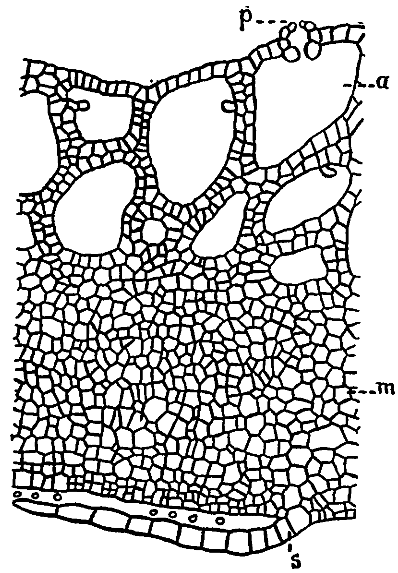

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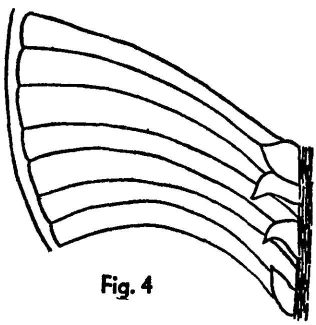

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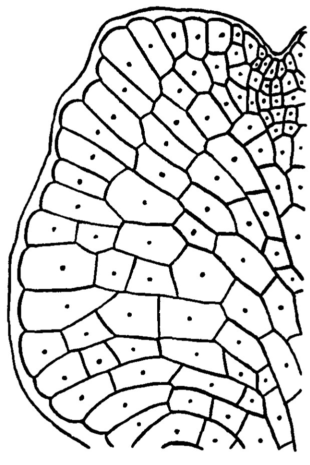

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Fig. 6

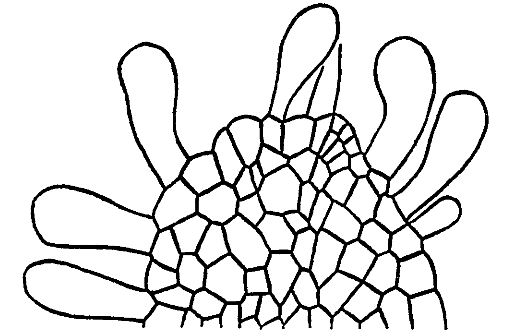


Fig. 7

FIG. 1.—Outline drawing of a transverse section of a young part of the thallus *a*, air chamber m, midrib region. s, scale. × 10 FIG. 2.—Outline drawing of a vertical section of the terminal portion of the thallus *a*, air chamber m, midrib region s, scale × 35 FIG 3 —Transverse section of a part of the thallus near the midline at a young stage The air chambers increase in size later. *a*, air chamber. m, midrib region p, airpore. s, scale × 80 FIG. 4 —View of the ventral surface of a wing of the thallus showing the length of the air chambers × 10 FIG 5 —View of the dorsal surface of a wing of the thallus showing the polygonal areas which represent the ends of the air chambers. The dots represent the air pores. × 10. FIG 6 —View of the internal opening of an air pore × 80. FIG 7 —Surface view of the edge of a young scale showing the projecting mucilage hairs. × 400.

thallus cut across the curving air chambers and only rarely show them in their full length, so that there appear to be two layers of air chambers in the central region and two or three layers in the wings (fig. 1).

Separating the air chambers are partitions two cells in thickness containing chloroplasts Short club-shaped colourless cells project into the air chambers, but these occur in small numbers only, not more than seven in a chamber. Filaments two or three cells in length sometimes replace the single projecting cells, most noticeably in the air chambers of the archegoniophore.

The ventral epidermal layer of the wings is uniseriate and almost colourless The dorsal epidermal layer is likewise uniseriate but is green except for the cells which bound the barrel-shaped air pores leading into the air chambers. The air pores are arranged in orderly fashion, one in the centre of each polygonal area. Each pore is surrounded by four tiers each of four cells (fig. 3). The whole structure projects as a low cone on the thallus surface and hangs pendulous in the air chamber The internal opening is large and almost square in outline (fig. 6).

From the ventral surface of the midrib arise two kinds of rhizoids and also plate-like scales Most of the rhizoids are wide, thin-walled rhizoids of a diameter of 37μ, growing straight down into the soil. Amongst them occur narrow, thick-walled rhizoids of a diameter of 9μ Pegs were not found in the narrow, thick-walled rhizoids on the vegetative portion of the thallus but occur in those present in the furrow of the archegoniophore The plate-like scales are colourless, multicellular structures, one cell in thickness, lying in a row on either side of the midrib (figs. 1, 2 and 3) The young scales are approximately triangular and acuminate, but are irregular in outline since unicellular, club-shaped mucilage hairs project from the margin (fig. 7) Later the hairs wither off and the scales become brown in colour.

Growth of the thallus is due to a single, wedge-shaped apical cell with four cutting faces which lies at the base of the apical notch (figs. 8, 9 and 10). The segments cut off on the ventral face give rise to the ventral part of the midrib. Those cut off on the dorsal face give rise to the dorsal part of the midrib and also to the open tissue with air chambers lying above the midrib. Segments cut off from the lateral faces give rise to the lateral portions of the midrib and to the open tissue containing air chambers which makes up the wings. The scales begin to develop from superficial ventral cells only one or two cells removed from the apical cell. The young scales curve over the apex and at this period their mucilage hairs are very conspicuous. The rhizoids do not develop till later, being found at a distance of 1 to 2 mm. from the apical cell although the rhizoid initial cells can be recognised earlier. The air chambers arise schizogenously close to the apex (fig 10) They appear in the subepidermal layer at a distance of three or four cells from the apical cell and increase in size as a result of the rapid growth and repeated divisions of the surrounding cells The curvature and overlapping of the air chambers occurs when the cells of the midrib region elongate (fig 2)

Cupules and gemmae

Cupules are found either on sterile thalli or on thalli which also bear archegoniophores. They lie on the middle line of the thallus in a linear series 3–5 mm. apart (Campbell, 1954, fig 1). The cupule is a green, circular, cup-shaped

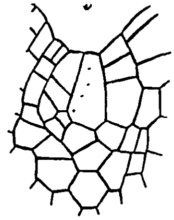
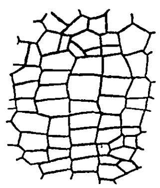


Fig. 8



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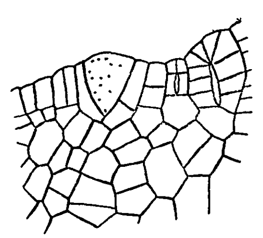

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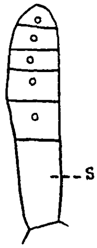

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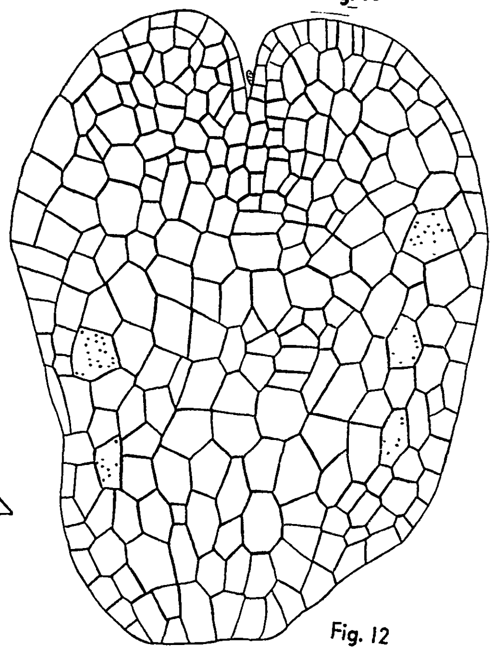

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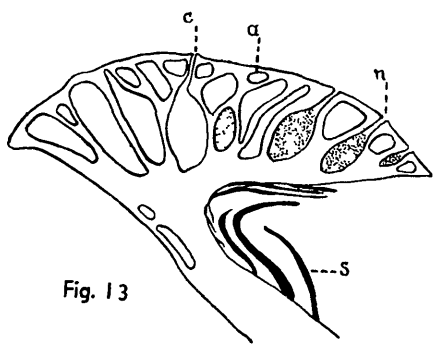


Fig. 13

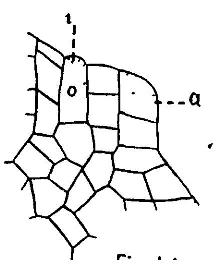
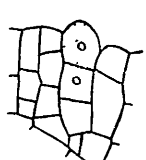


Fig. 14



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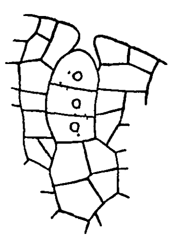

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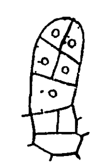

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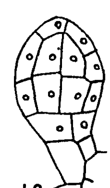


Fig. 18

FIG. 8.—Horizontal section of the apex of the thallus showing the apical cell (stippled). × 240 FIG. 9.—Transverse section of the apex of the thallus showing the apical cell (stippled) × 240. FIG. 10.—Vertical (sagittal) section of the apex of the thallus showing the apical cell (stippled) × 240. FIG. 11.—Young gemma attached by its stalk cell (s) to the floor of the cupule. × 380 FIG. 12.—Surface view of a gemma The tip of a mucilage hair at the apex and the colourless cells are stippled. × 180. FIG. 13.—Vertical section of an antheridiophore *a*, air chamber *c*, old antheridial cavity. n, cavity containing an antheridium s, scale × 40 FIG. 14.—Vertical section of the initial cell of an antheridium (i), showing its relation to an apical cell (*a*) of the antheridiophore. × 385. FIG. 15.—Vertical section of a young antheridium and the surrounding cells The antheridial initial cell has divided transversely into a basal cell and an outer cell. × 385 FIG. 16.—Vertical section of a young antheridium showing the file of three deeply staining cells formed from the outer cell. The rapid growth of the surrounding cells has left the young antheridium sunk in a cavity × 385 FIG. 17.—Vertical section of a young antheridium after the formation of vertical walls × 385 FIG. 18.—Vertical section of a young antheridium after the formation of periclinal walls × 385

structure 1·5–2 mm. in height and 3 mm in diameter at the top. Its floor is formed of the compact tissue of the midrib region and its sides consist of a layer of air chambers and their enclosing cells Vertical striations on the side walls of the cupule represent the partitions between the air chambers of the walls. The rim of the cup, at first, is fringed with minute, colourless, pointed teeth, but later these wither and turn brown. From the floor arise gemmae and short mucilage hairs.

The gemma originates from a floor cell as a protuberance which becomes cut off by a transverse wall It divides transversely into a stalk cell and a terminal cell. The stalk cell does not divide again. The terminal cell divides transversely 5–7 times (fig. 11) before vertical walls make their appearance The mucilage hairs are the same height as the stalk cells of the gemmae.

The mature gemma is lens-shaped, being one cell thick at the margin and up to four cells thick at the centre. At first all the cells have chloroplasts, but, as the gemma reaches full size, isolated surface cells at a distance of three cells from the margin appear colourless due to degeneration of the chloroplasts (fig 12) There is a single growing point at the anterior end, either in a median position or set obliquely In one isolated case two laterally-placed, growing points were present, one on either margin of the gemma as in *Marchantia* and *Lunularia;* but such a condition is not normal for *Marchasta* Cells immediately posterior to the growing point on one or on both flat faces project from the surface, each terminated by a club-shaped, mucilage hair which curves over the growing point.

The gemma eventually breaks away from its one-celled stalk and floats off in water. It begins to grow immediately it comes to rest on the soil. The colourless cells on whichever happens to be the ventral side develop into rhizoids. At first these are all of the thin-walled type with a diameter of 17μ. At the base of the rhizoids air spaces arise schizogenously in the thallus. Growth is rapid and within a week the thallus is ribbon-shaped Branching takes place when the thallus is approximately 1 mm long

THE STRUCTURE AND DEVELOPMENT OF THE ANTHERIDIOPHORE AND OF THE ANTHERIDIUM

The antheridiophore is terminal in position since an apical cell of the vegetative thallus functions as the apical cell of the young antheridiophore. The apical cell soon divides into two apical cells which take up a lateral position and these divide once more. The young antheridiophore is difficult to recognise for it is only slightly raised above the surface of the thallus. At first it has a convex head with decurved margins and is similar in appearance to a young archegoniophore.

The older antheridiophore has a slender, green stalk up to 8 mm high and a head which is practically flat on top (fig. 13). The stalk has air chambers on the morphologically dorsal side; on the opposite side are scales and either one or two deep grooves containing rhizoids mainly of the narrow, thick-walled type. The head is bilaterally symmetrical (Campbell, 1954, fig. 2), up to 3 mm. in diameter in the sagittal plane and up to 5 mm. in diameter in the plane at right angles. In general appearance it resembles an antheridiophore of *Marchantia polymorpha* L. with one side cut off. Scales and rhizoids are present on the ventral side and the dorsal portion has many air chambers. Embedded in the head are 50 to 60 antheridia, each sunk in a flask-shaped pit which opens by a narrow pore on the dorsal surface (fig. 13).

The antheridium arises from a superficial dorsal cell only two cells removed from the apical cell (fig. 14). This antheridial initial cell projects slightly above the surface of the thallus and soon divides transversely into a basal cell and an outer cell (fig. 15). The basal cell develops into the embedded foot portion of the antheridial stalk; the outer cell gives rise to the rest of the antheridium. The outer cell separates laterally from adjoining cells and soon becomes sunk in a cavity due to rapid upward growth of the surrounding cells. It divides transversely into a file of three cells easily recognisable because of their deeply-staining contents (fig. 16). The innermost cell of the file gives rise to the free portion of the stalk. Each of the two outer cells of the file divides by a vertical wall and then by another vertical wall at right angles to the first. There are now two tiers of four cells each (fig. 17). These cells now divide periclinally forming sterile jacket initials surrounding central fertile cells (fig. 18). The jacket initials divide by anticlinal walls forming the uniseriate jacket of the antheridium. The fertile cells divide repeatedly in the vertical and the transverse planes producing a large number of approximately cubical cells. Finally each cell divides by a diagonal division and the resulting protoplasts become transformed into spermatozoids.

The mature antheridium is conical in shape with a short stalk (figs. 19 and 20). The cavity in which it lies is bounded laterally by a single layer of cells and opens by a slightly raised, simple pore on the dorsal surface of the antheridiophore Projecting into the cavity at the base are 5 to 8 club-shaped mucilage cells.

The Structure and Development of the Archegoniophore and of the Archegonium

The archegoniophore or carpocephalum is terminal in position since an apical cell of the vegetative thallus functions as the apical cell of the young archegoniophore. The slender, green stalk is up to 20 mm. in length; on the morphologically ventral side it has a few scales and a deep groove filled with rhizoids, chiefly of the thick-walled type; on the morphologically dorsal side the tissue is open with large air chambers. The head is deeply cleft into four segments each of which is cut into two lobes. Occasionally there are eight segments, each bilobed. The lobes are so arranged that they all lie on the anterior side of the stalk with the result that the head is semicircular in outline (Campbell, 1954, fig. 2). It is convex above and about 4 mm. in radius when mature. The dorsal region is composed of air chambers and on the ventral side near the stalk there are scales and rhizoids.

When the archegoniophore first makes an appearance the head is only slightly raised above the level of the thallus. The apical cell divides to form two apical cells which are laterally placed and each of these by two successive divisions forms four apical cells, making eight in all. The apical cells are carried to the under side of the head by the rapid development and expansion of the dorsal zone of air chambers and lie close to the stalk. Each apical cell then functions in the following manner (figs. 21 and 23). Ventrally, that is on the side facing the stalk, it gives rise to compact tissue, with scales and rhizoids at the surface.

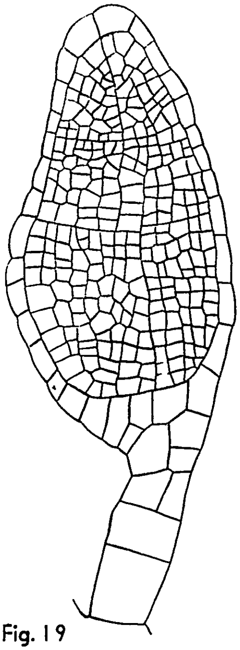
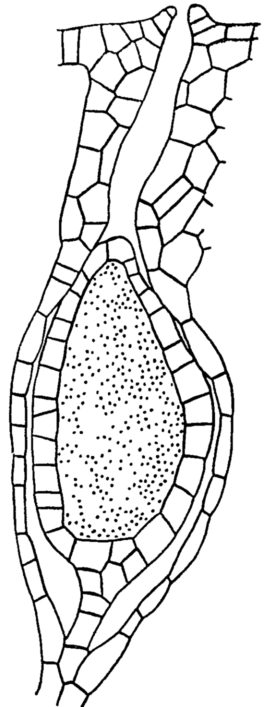


Fig. 19



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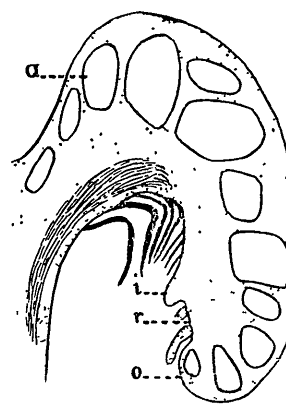

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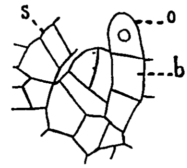

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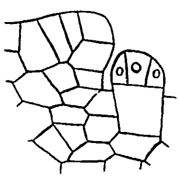

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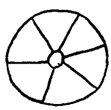

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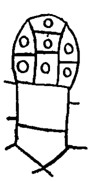

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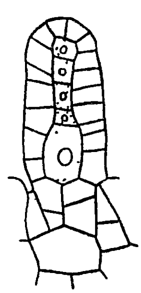

Fig. 26

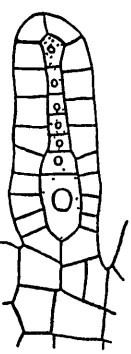

Fig. 27

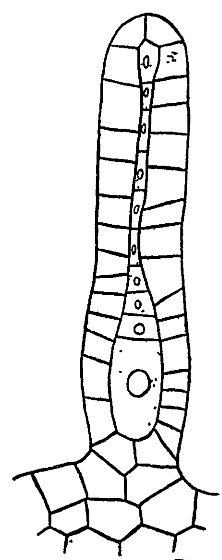

Fig. 28

FIG. 19.—Vertical section of a well-developed antheridium. × 385. FIG. 20.—Vertical section of an antheridial cavity containing a mature antheridium. × 385. FIG. 21.—Vertical section of one lobe of an archegoniophore. *a*, air chamber. i, inner portion of the involucre formed by the apical cell after the formation of the receptacle. o, outer portion of the involucre r, receptacle with archegonia. × 40. FIG. 22.—Vertical section of an apical cell of the archegoniophore, and of a young archegonium in which the initial cell has divided transversely into a basal cell (b) and an outer cell (o). s, part of a scale. × 390. FIG. 23.—Vertical section of an apical cell of the archegoniophore and of a young archegonium after the delimitation of the axial cell. This is the last archegonium to be formed on this receptacle and the apical cell is now giving rise to the innermost portion of the involucre × 390. FIG. 24.—Transverse section of the neck of a mature archegonium showing the canal surrounded by six vertical rows of cells. × 390. FIG. 25.—Vertical section of a young archegonium after the central cell has divided forming the primary canal cell and the primary ventral cell. × 390. FIG. 26.—Vertical section of a young archegonium after the primary canal cell has divided. × 390. FIG. 27.—Vertical section of a young archegonium after the primary ventral cell has divided. × 390. FIG. 28.—Vertical section of a fully developed archegonium. × 390.

Laterally, that is on either margin of the lobe, it gives rise to loose tissue containing air chambers so forming the sides of the involucre. Dorsally, that is on the side facing the periphery of the head, it gives rise to a flat receptacle of compact tissue bearing 8 to 10 archegonia formed in acropetal succession. The necks of the archegonia project downwards and the youngest archegonia are nearest the stalk. After the receptacle has been formed, the apical cell gives rise on its dorsal face to a limited zone of open tissue with air chambers; this tissue lies between the receptacle and the stalk of the archegoniophore, and it forms the innermost portion of the involucre. Finally the apical cell divides transversely and loses its identity. At this stage then there are eight receptacles on the under side of the head, each surrounded by a cylindrical sheath or involucre projecting downwards from the margin of the lobe. The involucre gradually grows forward around the receptacle, enclosing it except for a slit-like, bilabiate opening which extends along the length of the receptacle (Campbell, 1954, fig. 3).

The Archegonium

The initial cell of the archegonium is recognisable close to the growing apex. A cell cut off on the dorsal face of the apical cell divides transversely into a superficial cell and an inner cell. The superficial cell is the initial cell of the archegonium. It projects from the surface and divides transversely into a basal cell and a densely-staining outer cell (fig. 22). The basal cell gives rise to the base of the venter and the embedded portion of the archegonium; the outer cell gives rise to the rest of the archegonium. In the outer cell three inclined vertical walls are laid down in such a way as to cut off three peripheral cells from an axial cell (fig. 23). The peripheral cells give rise to the jacket of the archegonium, comprising the venter which is one cell in thickness and the neck composed of six vertical rows of cells (fig. 24).

The axial cell divides transversely into the primary cover cell and the central cell. The primary cover cell divides later by two vertical walls at right angles to each other and so forms the four cover cells at the top of the neck. The central cell divides transversely forming the primary canal cell and the primary ventral cell (fig. 25). The primary canal cell gives rise to a row of eight neck canal cells and the primary ventral cell gives rise to the ventral canal cell and the large egg (figs. 26, 27 and 28). Finally the canal cells with the exception of the egg disintegrate and the cover cells separate from one another. The neck of the mature archegonium is straight or curved, depending on its position with respect to the involucre.

The Structure and Development of the Sporogonium

The fertilized egg surrounds itself with a wall and then divides transversely into two cells (fig. 29). Each of these cells divides again transversely with the result that a row of four cells is formed (figs. 30 and 31). The basal cell of the row is the initial cell of the foot, the next cell gives rise to the seta, the next again gives rise to all of the capsule except for the top part of the jacket which is derived from the terminal cell of the row.

Further development takes place in the following manner (figs. 32–35). In the foot initial cell an approximately vertical wall is laid down and then further walls are formed at varying angles. The foot eventually becomes about ten cells in diameter and about 12 cells high. Its surface cells enlarge and press into

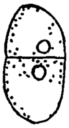

Fig. 29

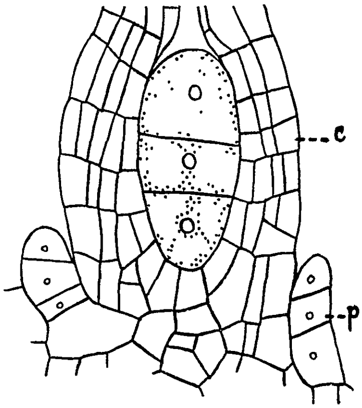

Fig. 30

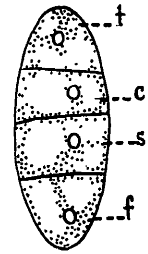

Fig. 31

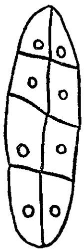

Fig. 32

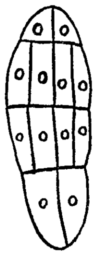

Fig. 33

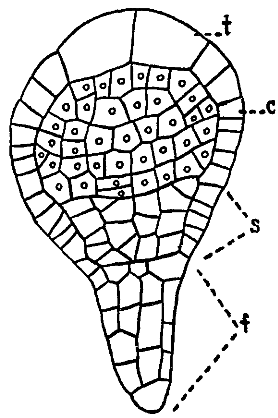

Fig. 34

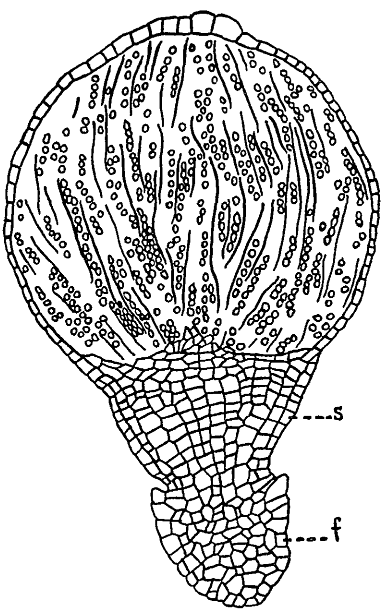

Fig. 35

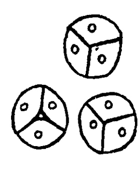

Fig. 36

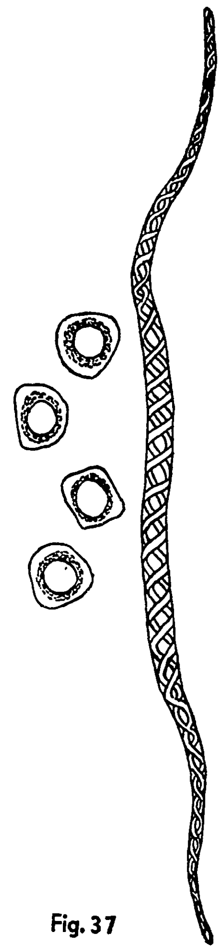

Fig. 37

FIG. 29.—Vertical section of a two-celled sporogonium × 385. FIG 30 —Vertical section of a three-celled sporogonium enclosed by the enlarging calyptra (c). The pseudoperianth (p) is beginning to develop. × 385 FIG. 31.—Vertical section of a four-celled sporogonium. c. initial cell of the capsule. f, initial cell of the foot. s, initial cell of the seta t, terminal cell. × 385. FIG. 32.—Vertical section of a young sporogonium showing vertical walls. × 385. FIG 33.—Vertical section of a young sporogonium after the delimitation of the endothecium and the amphithecium in the capsule region. × 385. FIG. 34.—Longitudinal section of a somewhat older sporogonium c, capsule region. f, foot region. s, seta region. t, terminal cells. × 240. FIG. 35.—Longitudinal section of a sporogonium showing spore mother cells and elater cells. f, foot s, seta. × 75. FIG. 36.—Spore tetrads × 380. FIG. 37.—Ripe spores and an elater. × 375.

the adjoining cells at the base of the archegonium and all of its cells have densely staining contents. In the initial cell of the seta two successive vertical walls are formed at right angles to each other. Then periclinal walls are laid down separating peripheral cells from central ones. The peripheral cells divide by anticlinal walls. The central cells divide mainly by vertical and transverse walls producing rectangular cells regularly arranged in rows about 12 cells in height (fig. 35). In the capsule initial cell the first wall is a vertical one and this is soon followed by a second vertical wall at right angles to the first. Periclinal vertical walls then form and delimit an endothecium from an amphithecium (fig. 33). The amphithecium divides by anticlinal walls only and gives rise to the lateral portion of the uniseriate jacket of the sporogonium. The endothecium divides repeatedly in the transverse and the vertical planes and gives rise to the sporogenous tissue. Meanwhile the terminal cell of the original four-celled row divides by a vertical wall and then does not divide again for some time. The terminal cells remain conspicuously large while all the other cells of the sporogonium have become smaller as a result of repeated divisions (fig. 34) Later, when the spores are forming, the terminal cells divide by anticlinal walls and form the uniseriate cap of the sporogonial jacket.

As the capsule enlarges it becomes globose. The sporogenous cells begin to stain deeply and to become fusiform in shape. Some divide transversely forming a file of spore mother cells while others elongate greatly and form elaters. The spore mother cells round off and separate from one another (fig. 35). Each gives rise to a tetrad of spores (fig. 36). No lobing of the cytoplasm occurs during spore formation. In the wall of the mature spore three layers are recognizable (fig. 37). There is a thin inner layer (endosporium), a thick middle layer (mesosporium) and a papery, wing-like outer layer (exosporium) which becomes wrinkled as it dries. The elaters vary in length from 240μ to 625μ; they are 9μ in diameter at the widest part and taper gradually towards the tips. When mature they have two spiral bands of thickening on the wall (fig. 37). As the capsule ripens the lateral walls of the jacket cells develop bands of thickening in the form of rings or halfrings (fig. 38). In the cap region the cells are of greater radial diameter and the thickening is laid down irregularly.

Only one sporogonium develops to each lobe of the archegoniophore While it is developing it is surrounded by a calyptra, a pseudoperianth and an involucre.

The calyptra develops from the venter of the archegonium. Transverse and periclinal divisions take place in the venter immediately after fertilization (fig. 30) and continue until, at the stage when the endothecium is beginning to enlarge and divide, the calyptra has reached a maximum width of eight cells. Thereafter there occurs a flattening and absorption of the innermost cells of the calyptra and this process gradually extends outwards until by the time the spore mother cells are formed the calyptra is merely a withered, structureless sheath

The pseudoperianth begins to develop as soon as the fertilized egg commences division (fig. 30). It arises from the receptacle tissue at the base of the archegonium as a cylindrical sheath one cell in thickness and gradually grows forward until it encloses the calyptra and the developing sporogonium (fig. 39)

The involucre originates at the time of the formation of the receptacle as has been described above. It enlarges by the intercalary growth of the receptacle tissue at its base and of the tissue which makes up its side walls. As the involucre develops it projects obliquely downwards and outwards from the head as a cylindrical sheath, shaped like a cocoon (fig. 39). On the under side near the periphery is a narrow slit-like opening running for a short distance inwards towards the axis of the head (Campbell, 1954, fig. 3). The outer surface of the involucre is marked by striations curving more or less vertically downwards; these mark the partitions between the long, narrow air chambers present in the walls. The involucre is united with the pseudoperianth for a distance of 80μ at the base, both structures being carried downwards by the intercalary growth of the adjoining receptacle tissue. The pseudoperianth is united with the

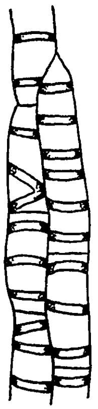

Fig. 38

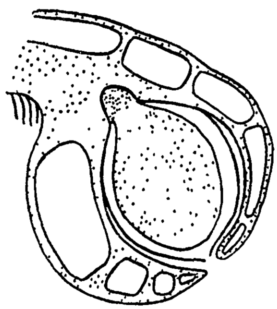

Fig. 39

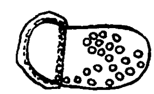

Fig. 40

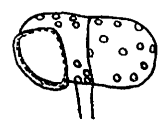

Fig. 41

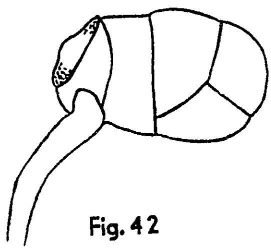

Fig. 42

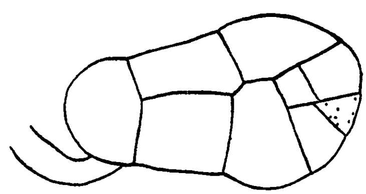

Fig. 43

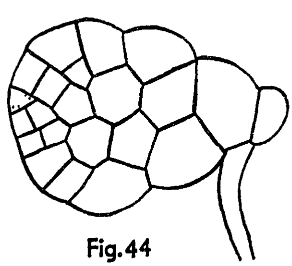

Fig. 44

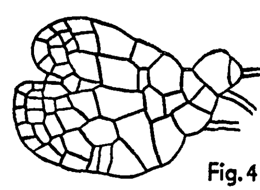

Fig. 45

FIG. 38.—Jacket cells of the ripe capsule. × 225 FIG. 39.—Outline drawing of a longitudinal section of a nearly mature sporogonium enclosed by the pseudoperianth and involucre The calyptra has withered. × 15. FIGS. 40 and 41.—Germinating spores, ten days after sowing. × 380. FIG. 42.—Germinating spore showing the formation of an apical cell. × 380. FIG. 43.—Germinating spore three weeks after sowing; the apical cell has cut off two segments × 380. FIG. 44.—Stage at four weeks after the sowing of the spores. × 250. FIG 45.—Surface view of a heart-shaped gametophyte five weeks after the sowing of the spores. × 90.

calyptra for a somewhat longer distance from the base, again due to the intercalary growth of the receptacle tissue.

When the sporogonium is nearly mature the slit-like pore of the involucre opens as a small diamond-shaped mouth. The pseudoperianth reaches almost to the mouth and is closely appressed to the sporogonium which it encloses The stalk of the sporogonium elongates a little and carries the dark-brown capsule to the mouth of the involucre. The sporogonium does not lie vertically but is placed obliquely and points downwards in the direction of the periphery of the head (fig. 39). The capsule now dehisces at the apex into four or five valves which are held in position by the pseudoperianth and the involucre. Some of the brown spores are shed by the twisting movements of the elaters Then, as a result of the further elongation of the stalk cells, the capsule is gradually carried beyond the pseudoperianth and just outside the mouth of the involucre The valves now split right to the circular base and spread out flatly in the form of a star lying against the involucre (Campbell, 1954, fig. 3) At this stage the remainder of the spores are shed.

Germination of the Spore

Freshly-gathered spores were sown on two types of substratum. Some were sown on the outside of sterilized flower-pots which had been filled with sterilized sphagnum moss and inverted. Others were sown on sterilized turves cut from the trunk of a tree-fern stem. Growth was satisfactory in both cases. The cultures were watered from below with sterilized Knop's solution and kept in a Wardian case.

Germination commences in seven to ten days The two outer coats of the spore are ruptured and the protoplast surrounded by the innermost spore coat grows out as a single cell containing chloroplasts (fig 40). This cell soon gives rise to a filament of two cells and to a rhizoid (fig 41). Further growth usually produces a filament of three or four cells, but, if the basal cells divide in an axial plane, a flat plate two cells broad is formed Then in the terminal cell there is delimited an apical cell with two lateral cutting faces (fig 42), and this cell cuts off five or six segments (figs. 43 and 44). The gametophyte at this stage looks like the young prothallus of a leptosporangiate fern Some five weeks after the spores have been sown the apical cell becomes wedge-shaped and the gametophyte assumes a heart-shaped form (fig. 45) Soon after this the gametophyte becomes more than one cell thick and develops air chambers and multicellular scales.

Discussion

Marchasta clearly belongs to the order Marchantiales of the Hepaticae because it shows the following characters The thallus in its internal structure shows differentiation into a dorsal photosynthetic region containing air chambers and a compact ventral zone which is almost colourless On the ventral surface there are multicellular scales and two types of rhizoids The antheridial initial cell divides transversely several times and forms a file of cells prior to the formation of vertical walls The archegonium has a six-rowed neck and a uniseriate venter The sporogonium has a uniseriate jacket The only feature in which *Marchasta* differs from the typical Marchantiales is in the absence of brown oil-bodies in the thallus.

The order Marchantiales includes several families, one of which is the Marchantiaceae. According to some authors (Campbell, 1940, 93) the Marchantiaceae includes all the genera which have a stalked archegoniophore, and the family is subdivided into three subfamilies, namely Astroporae, Operculatae and Compositae. Other authors (Verdoorn, 1932, 430) raise the three subfamilies to the rank of families and refer to the Compositae as the Marchantiaceae *Marchasta* shows affinity with the Marchantiaceae (in the restricted sense) and the present author has classified it in this family.

Apart from characters which it shares in common with other members of the Marchantiales, *Marchasta* resembles *Marchantia*, the type genus of the Marchantiaceae, in several respects. The upper surface of the thallus is marked out into polygonal areas, each with a barrel-shaped air pore at its central point. The air chambers of the thallus have no secondary walls. The gemma-cups which are found on the dorsal surface resemble those of *Marchantia* in general appearance and the gemmae develop in the same manner Both the antheridiophores and the archegoniophores are stalked and represent branch-systems of the thallus. The head of the archegoniophore carries several receptacles, each with several archegonia. The sporogonium has a well-developed foot, a seta which does not elongate greatly, and a terminal capsule dehiscing into valves. It is surrounded by a calyptra, by a pseudoperianth and by an involucre. The capsule has the walls of the jacket cells strengthened by annular or half-ring shaped bands and contains well-developed elaters intermixed with the spores.

On the other hand, *Marchasta* differs from *Marchantia* in several features. Most of these, however, can be paralleled in other members of the Marchantiaceae, as is indicated below The air chambers of *Marchasta* are of a different type from those of *Marchantia*, since in the former genus the air chambers are large and the hairs within them lack chloroplasts. They resemble in some degree the type of air chamber which occurs in *Stephensoniella* (Kashyap, 1914) and in *Bucegia* (Schiffner, 1908) and is found also in some other families of the Marchantiales; but in this latter type there are usually no free hairs, the air pores of the thallus, except in *Bucegia*, are not barrel-shaped, and the partitions between the air chambers are typically uniseriate. The ventral scales of *Marchasta* have mucilage hairs on their margins when they are young; these hairs are similar to those present on the basal portions of the scales of *Conocephalum* (Cavers, 1904). Growth of the thallus in *Marchasta* is due to the activity of a single, wedge-shaped, apical cell with four cutting faces, whereas in *Marchantia* there is reported to be a transverse row of apical cells (O'Hanlon, 1926). However, the single wedge-shaped type of apical cell is known to occur in the Marchantiaceae and has been described for *Preissia* (Haupt, 1926). The gemma of *Marchasta* has a single growing point, often obliquely placed, and adjacent to the growing point are mucilage hairs, *Marchantia*, on the other hand, has a gemma with two, laterally-placed growing points Adventitious branches arise frequently in *Marchasta*, and although not found in *Marchantia*, they occur in other members of the Marchantiaceae (Stephani, 1900)

There are differences, too connected with the reproductive structures. The monoecious condition in *Marchasta* (Campbell, 1954) contrasts with the dioecious condition in *Marchantia* In *Marchasta* the archegoniophore has no projecting rays alternating with the receptacles of the head, such rays are a prominent feature of *Marchantia* except in a few species which it has been suggested should be placed in a separate genus (Douin, 1918). The involucre of *Marchasta* is a cylindrical sheath with a narrow, slit-like opening and it encloses the single sporogonium which develops on a receptacle. It is very different from that of *Marchantia* where the involucre takes the form of two curtain-like flaps, one on either side of the several sporogonia which develop on a receptacle. In the development of the sporogonium in *Marchasta* the terminal cells of the jacket are set apart at an early stage. A similar condition exists in *Dumortiera velutina* Schiffn. (Campbell, 1918) but in this case the cap eventually becomes 2–3 cells thick. When the sporogonium of *Marchasta* is mature, the valves of the capsule separate from one another right to the base and flatten back into a star shape This type of open capsule may be compared with that of *Wiesnerella denudata* Mitten (Campbell, 1918), although in *Wiesnerella* the stalk of the sporogonium is of greater length. The spores of *Marchasta* have a broad wing. Germination takes place by rupturing of the outer coats and differs from that of *Marchantia* where the spore enlarges and divides without rupture of the spore coats (O'Hanlon, 1926).

From the foregoing account it is evident that, although there are certain similarities between *Marchasta* and *Marchantia,* there are also marked dissimilarities. Details of structure and development are less perfectly known for some other genera of the Marchantiaceae and in these cases it is more difficult to institute comparisons. However, sufficient evidence is available to indicate that *Marchasta* does not correspond with any of the already-described genera Consequently it has been necessary to constitute the new genus.

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Addendum

This genus has also been described by H. Persson in a paper entitled "On *Neohodgsonia* H. Perss., the new hepatic genus from New Zealand and Tristan da Cunha." *Bot. Not.* Häfte I: 39–44, 1954.